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Morphological and molecular evidence reveal a new Asian leaf litter toad of the genus *Leptobrachella* Smith, 1925 (Anura, Megophryidae) from the northeastern hills of Yunnan, China

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Abstract

The genus *Leptobrachella* Smith, 1925 includes 110 species and is the most diverse genus of the family Megophryidae. The recent and rapid description of numerous new species of *Leptobrachella* suggests that its species diversity is underestimated. The Northeastern Hills of Yunnan, China, are located in the Wumeng Mountain region, bordering Sichuan and Guizhou provinces. Compared to the other two neighboring provinces in the Wumeng Mountain region, the diversity of *Leptobrachella* in the Northeastern Hills of Yunnan has attracted less attention. During herpetological surveys in 2024, three *Leptobrachella* specimens were collected from the Northeastern Hills of Yunnan. The molecular phylogenetic analyses indicate the presence of a separate and previously unknown lineage in the *L. oshanensis* complex. Morphologically, they are distinguishable from their congeners based on differences in body size, degree of webbing and fringing on the toes, ventral skin texture, and iris coloration in life. Herein, based on the integration of morphological comparisons and phylogenetic reconstruction, we describe a new species of *Leptobrachella* from the Northeastern Hills of Yunnan. Our discovery increases the number of *Leptobrachella* species recorded in China to 47 and the total number of known species in the genus to 111. Our study further confirms that species diversity in the Northeastern Hills of Yunnan is underestimated, thus highlighting the need to further strengthen fieldwork and study in the future.

Key Words

Biodiversity, frog, *Leptobrachella weixinensis* sp. nov., new species, Yunnan Province

Introduction

The Asian leaf litter toads of the genus *Leptobrachella* Smith, 1925 (Anura, Megophryidae) were originally described by Smith (1925), with the type species *Leptobrachella mjöbergi* Smith from Sarawak, Malaysia. The species in this group had previously been classified into different genera, i.e., *Paramegophrys* Liu, 1964, *Carpophrys* Sichuan Biological Research Institute, 1977, and *Leptolalax* Dubois, 1980, until Chen et al. (2018) placed these genera as junior synonyms of *Leptobrachella* based on large-scale molecular analyses. These species are generally small-sized, forest-floor specialists that inhabit montane evergreen forests throughout tropical and subtropical Asia, ranging from northeastern India and southern China to Southeast Asia (Frost 2025).

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Species diversity within the genus has increased rapidly in recent years. Currently, the genus contains 110 species, with over 50% of the recognized species described in the past decade (e.g., Chen et al. 2021a, 2024; Cheng et al. 2021; Lin et al. 2022; Luo et al. 2022; Liu et al. 2023; Shi et al. 2023; Li et al. 2024; Frost 2025; Wu et al. 2025). Some recent studies have shown that there are many cryptic species in this genus (Chen et al. 2018, 2020; Wu et al. 2022). These studies indicate that the species diversity of the genus *Leptobrachella* is underestimated and that there may still be a large number of undiscovered cryptic species.

During recent field surveys in the mountainous areas of northeastern Yunnan, which border Guizhou and Sichuan provinces, we collected three adult male specimens of *Leptobrachella*. Based on morphological and molecular phylogenetic analyses, these individuals were found to differ from all other known congeneric members. Considering both their morphological differences and their genetic allocation and divergences, these specimens are described herein as a new species of the genus *Leptobrachella*.

Materials and methods

Sampling

During a field survey at Shizigou Village, Zhaxi Town, Weixin County, Zhaotong, Yunnan Province, China, in June 2024 (Fig. 1), three adult male specimens of *Leptobrachella* were collected and photographed. Sex was determined by the presence of internal vocal sac openings. The specimens were then euthanized, fixed in 10% formalin, and subsequently stored in 75% ethanol for 24 hours. Liver tissues were taken and preserved in 95% alcohol. The procedures for DNA tissue sampling and specimen fixation followed the protocols detailed in Chen et al. (2021b). Voucher specimens were deposited at Nanjing Normal University (NNU), China. Research protocols were approved by Nanjing Normal University (IACUC-2025068).

DNA extraction, PCR, and sequencing

Total genomic DNA was extracted from liver tissue stored in 95% ethanol using the standard phenol-chloroform extraction protocol (Sambrook et al. 1989). Partial sequences of the mitochondrial 16S rRNA gene from the new samples were amplified and sequenced using the primer pairs (5'–3') 16SAR (CGCCTGTTTAYCAAAAACAT) and 16SBR (CCGGTYTGAACTCAGATCAYGT) (Kocher et al. 1989). PCR amplification was performed in a 25 µl reaction volume with the following cycling conditions: initial denaturation at 94 °C for 5 min; 35 cycles of denaturation at 94 °C for 40 s, annealing at 55 °C for 40 s, and extension at 72 °C for 1 min; followed by a final extension at 72 °C for 10 min. PCR products were purified using the Gel Extraction Mini Kit (Watson BioTechnologies, Shanghai, China) and sequenced in both directions using the BigDye Terminator Cycle Sequencing Kit on an ABI PRISM 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA). All sequences were assembled from forward and reverse reads and edited manually using DNASTAR LASERGENE 7.1. Newly generated sequences were deposited in GenBank (Suppl. material 1).

Phylogenetic analyses

To determine the phylogenetic relationships among *Leptobrachella*, homologous sequences of all available *Leptobrachella* species were downloaded from NCBI GenBank (Suppl. material 1). Ingroup samples consisted of 83 individuals representing 44 nominal species and included three samples from the new Yunnan population. *Leptobrachium huashen* and *Megophrys montana* were chosen as outgroups based on previous phylogenetic studies (Chen et al. 2018). New sequences were aligned with GenBank data using MUSCLE 3.8 (Edgar 2004), inspected visually for accuracy, and trimmed to minimize missing data in MEGA 6.0 (Tamura et al. 2013).

Bayesian inference (BI) and maximum likelihood (ML) methods were used to infer phylogenetic trees. The best-fit model of nucleotide substitution was determined using the Bayesian information criterion (BIC) in jModelTest 2.1.7 (Darriba et al. 2012). The GTR+I+G model was selected as the best-fit model for 16S rRNA. Both BI and ML analyses were performed using the CIPRES Science Gateway (Miller et al. 2010). For BI analysis, two independent runs were conducted using Metropolis-coupled Markov Chain Monte Carlo (MCMCMC), each with four chains (three heated and one cold). Chains were run for 10,000,000 generations, with the cold chain sampled every 1,000 generations. The first 25% of each run was discarded as burn-in. Convergence was assessed in Tracer v1.6 (Rambaut et al. 2014) by ensuring that the average standard deviation of split frequencies was below 0.01 and that effective sample sizes (ESS) for all parameters exceeded 200. ML analyses were conducted using RAxML-HPC BlackBox 8.2.10 (Stamatakis 2014) on the CIPRES Science Gateway (Miller et al. 2010). Analyses used the GTR+Gamma model and included 1,000 bootstrap pseudoreplicates. Uncorrected pairwise distances (p-distances) between species were calculated using 16S rRNA sequences in MEGA 6.0 (Tamura et al. 2013).

Morphology

Three preserved adult specimens were examined and measured to the nearest 0.1 mm using digital calipers. Morphological terminology followed Fei et al. (2009) and Poyarkov et al. (2017). The following measurements were taken: snout-vent length (SVL), measured from tip of snout to vent; head length (HDL), measured from tip of snout to jaw angle; maximum head width (HDW), measured as head width at its widest point; snout length (SNT), measured from tip of snout to anterior corner of eye; tympanum-eye

Figure 1. Geographical location of the type locality of *Leptobrachella weixinensis* sp. nov. in Weixin County, Yunnan Province, China (red pentagram).

distance (TED), measured as the distance from anterior border of tympanum to posterior corner of eye; width of upper eyelid (UEW); tympanum diameter (TD), measured as maximal diameter of tympanum; distance from nostril to eye (DNE), measured as distance from the anterior corner of eye to nostril center; snout–nostril distance (SN), measured as distance from nostril center to snout tip; internarial distance (INS), measured as distance between nares; interorbital distance (IOD), measured at narrowest point between eyelids on top of head; eye diameter (ED), measured as the distance between corners of eye; distance between anterior orbital borders (IFE), measured as the shortest distance between the anterior corners of eyes; distance between posterior orbital borders (IBE), measured as the shortest distance between posterior corners of eyes; forearm length (FAL), measured from elbow to wrist; hand length (HL), measured as the distance from the proximal edge of inner metacarpal tubercle to the tip of third finger; thigh length (THL), measured from cloaca to knee; tibia length (TL), measured as the distance from knee to heel; TOL (length of tarsus); foot length (FL), measured as the distance from the proximal end of the inner metatarsal tubercle to the tip of the fourth toe; inner metatarsal tubercle length (IMTL); first to fourth finger lengths (1–4FL); and first to fifth toe lengths (1–5TL).

Result

The final aligned dataset of 16S rRNA nucleotide sequences contained 85 individuals with 512 bp (including outgroups). Among the 512 sites, 312 were conserved and 196 were variable, of which 164 were identified as potentially parsimony-informative (excluding outgroups).

The BI and ML phylogenetic trees yielded essentially identical topologies, with relatively high nodal support values for most terminal nodes, except for the basal relationships within *Leptobrachella*, which were poorly resolved (Fig. 2). The phylogenetic analysis showed that the monophyly of *Leptobrachella* was well supported (BPP = 0.99, BS = 74; Fig. 2). As shown in the tree (Fig. 2), the genus *Leptobrachella* forms four major clades (clades A–D); however, two clades were poorly supported, and the relationships among these clades were unresolved. Among these, the monophyly of the *L. oshanensis* complex was well supported (clade A; BPP = 1, BS = 79). All newly collected samples from Yunnan Province formed a distinct, well-supported monophyletic clade (BPP = 1, BS = 100; Fig. 2), which was nested within the *L. oshanensis* complex with strong support (clade A; BPP = 1, BS = 79). This lineage clustered with *L. bijie*, *L. jinyunensis*, and *L. chishuiensis* from Chongqing City and Guizhou Province with strong support (BPP = 0.99, BS = 71; Fig. 2).

The genetic distances based on the 16S gene among species of *Leptobrachella* are presented in Suppl. material 2 . The smallest genetic distance between the Weixin population and other *Leptobrachella* species was 2.5% (*L. chishuiensis*, see Suppl. material 2). This value is comparable to the divergences among the nearest neighbor pairwise genetic distances of described *Leptobrachella* species, which ranged from 1.1% (*L. bourreti* and *L. dushanensis*) to 9.0% (*L. khasiorum* and *L. yingjiangensis*, as well as *L. wulingensis* and *L. yingjiangensis*).

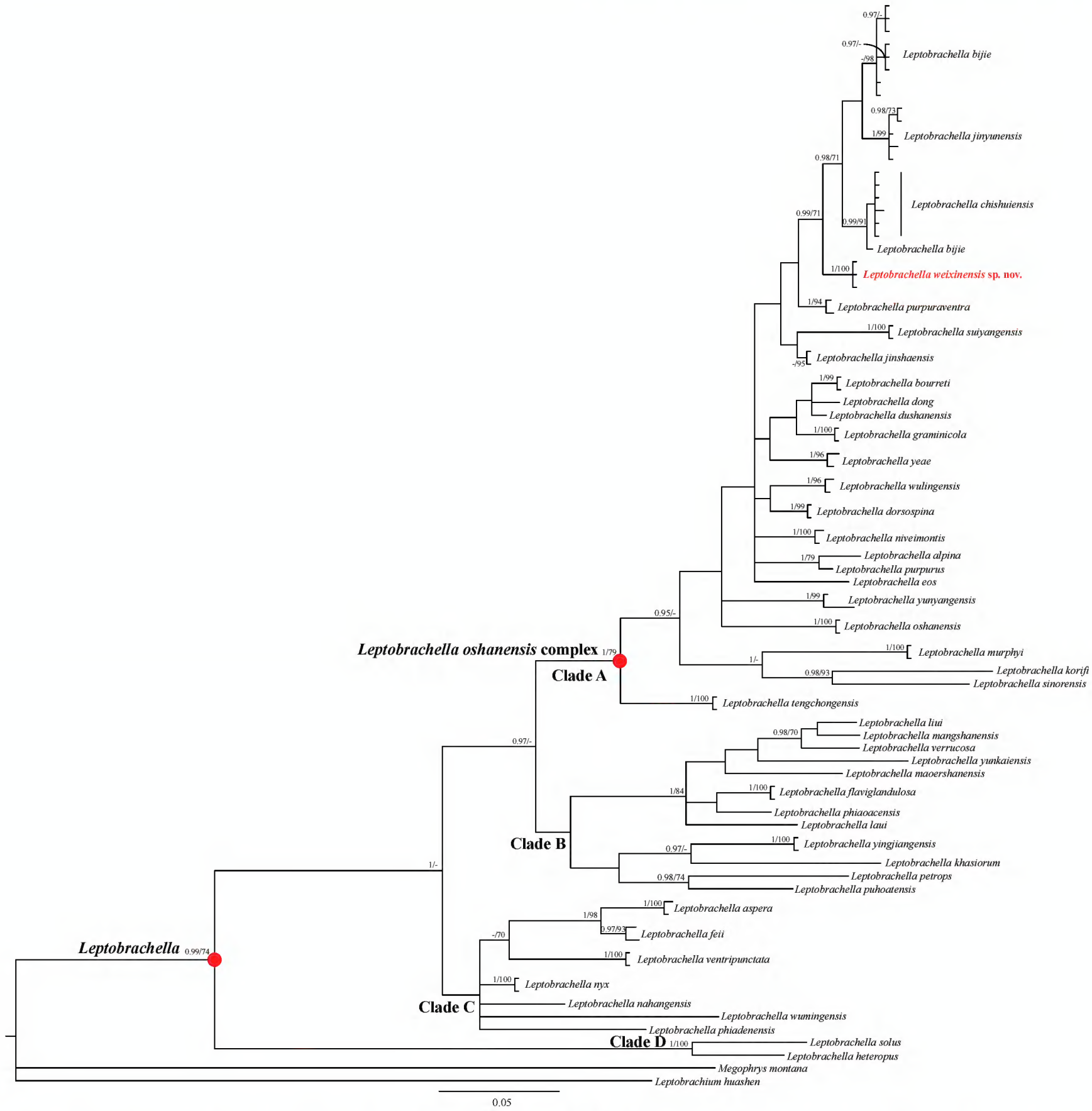

Figure 2. Phylogram of *Leptobrachella* inferred from a 16S rRNA mtDNA gene fragment. A "–" denotes Bayesian posterior probabilities (BPP) < 0.95 and bootstrap support (BS) < 70. Nodes without any numbers or symbols represent low support values (BS < 75% and BPP < 0.95). The new samples for the present study are indicated by the red font.

Morphologically, the new specimens differed in a number of taxonomically important diagnostic characters from other congeners. Thus, both mtDNA and morphological analyses clearly indicate that this population represents a separately evolving lineage and an undescribed species, which we formally describe below.

Taxonomic account

***Leptobrachella weixinensis* sp. nov.**

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Figs 3, 4, Table 1

Holotype. • NNU 040615, an adult male collected from Shizigou village, Zhaxi Town, Weixin County, Zhaotong, Yunnan Province, China (27.84730°N, 105.02633°E; elevation 1280 m a.s.l.), collected by Lu Chen on 15 June 2024.

Paratypes. • Two males, NNU 040602 and NNU 040603, collected at the same locality and with same collection information as the holotype.

Etymology. The specific epithet "weixinensis" is given as a noun in apposition and refers to the name of the Weixin County in Yunnan Province, China, where the new species occurs. We suggest the English common name "Weixin Leaf Litter Toad" and the Chinese common name "威信掌突蟾" (Wēi Xìn Zhǎng Tū Chán).

Diagnosis. *Leptobrachella weixinensis* sp. nov. is assigned to the genus *Leptobrachella* morphologically by the presence of small size, presence of macroglands (supra-axillary, femoral, and ventrolateral glands), vomerine teeth absent, rounded finger tips, and presence of an elevated inner metacarpal tubercle not continuous to the thumb (e.g., Dubois 1980; Ohler et al. 2011; Rowley et al. 2013). The new species can be further distinguished from its congeners by the combination of: (1) small body

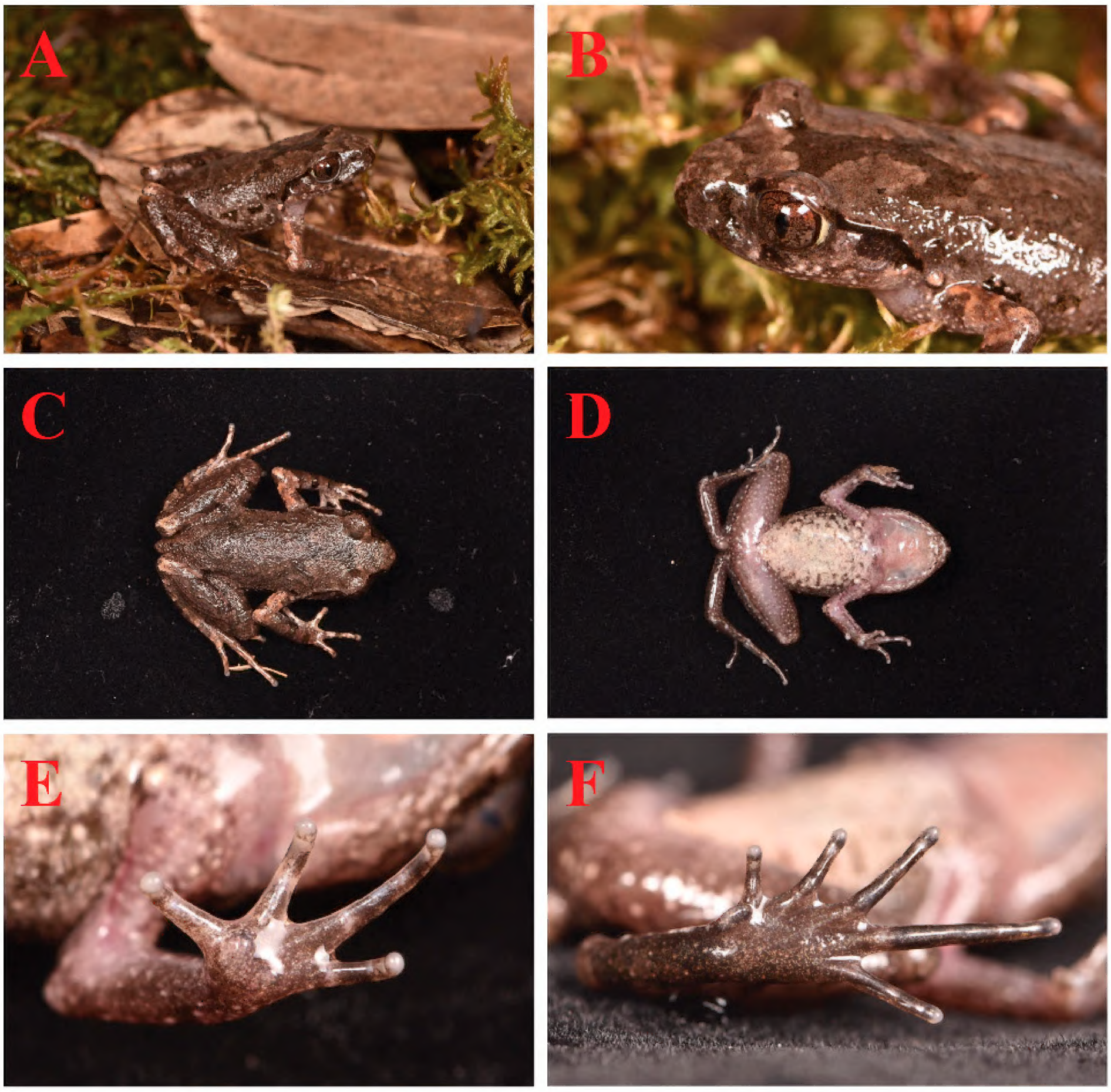

Figure 3. Holotype of *Leptobrachella weixinensis* sp. nov. (NNU 040615) in life. **A.** Lateral view; **B.** Lateral view of head; **C.** Dorsal view; **D.** Ventral view; **E.** Thenar view of the right hand, and **F.** Plantar view of the right foot. Photos by Yun-He Wu.

size (SVL 28.2–29.7 mm in three males); (2) interorbital space wider than internarial distance; (3) upper margin of tympanum incontact with supratympanic ridge; (4) tibiotarsal articulation reaches the nostril when hindlimb is stretched along the side of the body; (5) heels overlapping; (6) toes with rudimentary webbing and narrow lateral fringes; (7) flanks with large irregular black spots; (8) iris distinctly bicolored, typically orange in upper half, silver white in lower half; (9) ventral surface of throat, chest, and belly creamy white; chest and abdomen with distinct dark patches; (10) supratympanic ridge distinct with reddish-brown pigmentation.

Description of holotype (Table 1). NNU 040615, sexually mature male, body size small, SVL 28.2 mm; head length (HDL 10.0 mm) almost equal to head width (HDW 10.1 mm); head triangular in dorsal view; snout short (SNT/HDL 38.0%), snout round in both dorsal view and profile, projecting beyond margin of lower jaw (Fig. 3A, B); oval-shaped nostril closer to tip of snout than to anterior margin of eye; canthus rostralis indistinct; loreal region slightly concave; eyes large (ED/HDL 36.0%), protuberant in both dorsal and lateral views; eye diameter twice of the maximum tympanum diameter (TD/ED 200%) and subequal to snout length (ED/SNT 94.7%); tympanum distinct, rounded, tympanic ring slightly elevated relative to skin of temporal region (Fig. 3); upper margin of tympanum incontact with supratympanic ridge; eye-tympanum distance less than twice as long as maximum tympanum diameter (TED/TD 55.6%); pupil vertical; interorbital space (IOD 3.3 mm) flat, wider than internarial distance (INS 2.4 mm) and width of upper eyelid (UEW 2.8 mm); vomerine teeth absent; tongue with shallow notch at posterior tip; vocal sac openings slit-like, paired, located posterolaterally

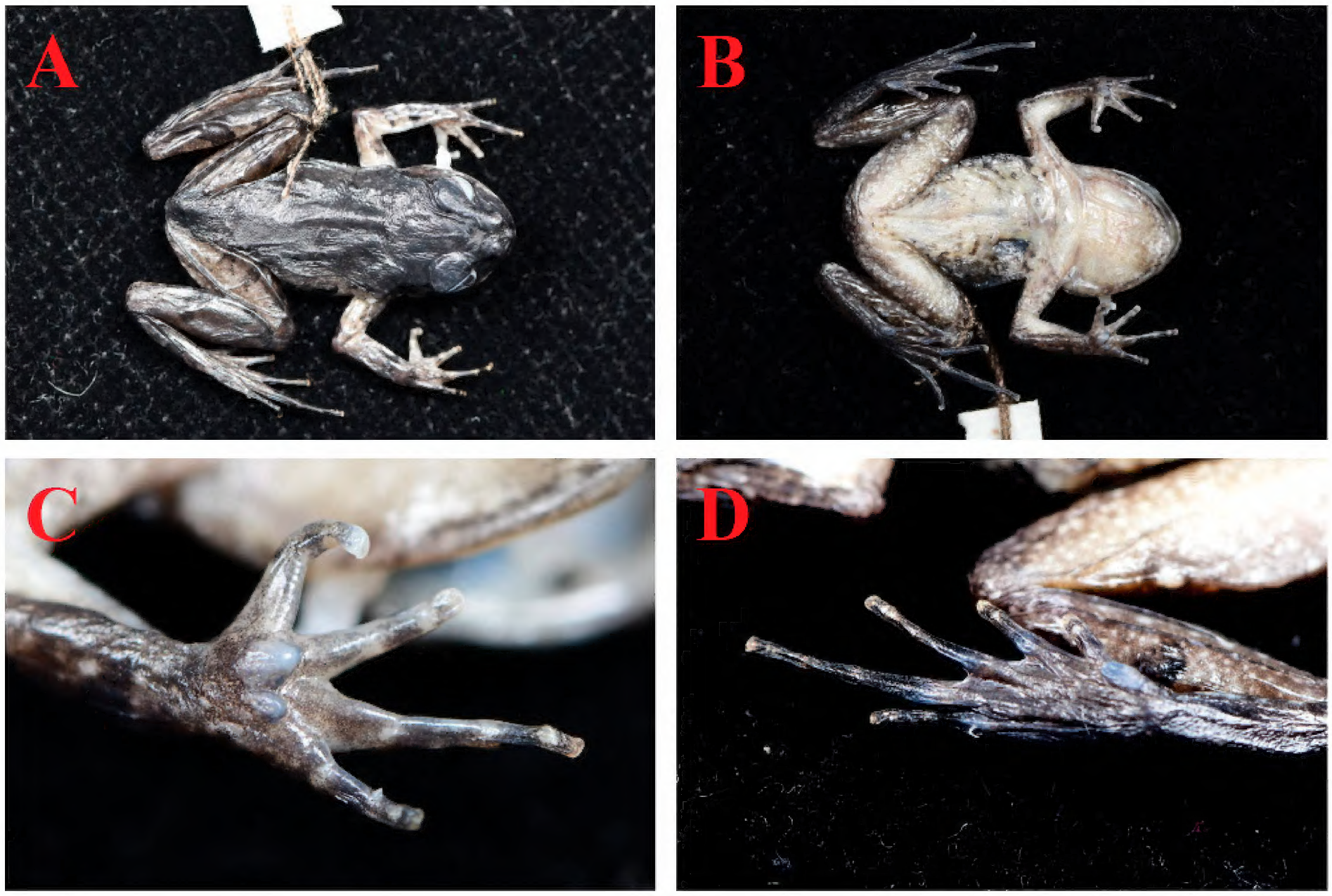

Figure 4. Holotype of *Leptobrachella weixinensis* sp. nov. (NNU 040615) in preservative. **A.** Dorsal view; **B.** Ventral view; **C.** Thenar view of the right hand; **D.** Plantar view of the right foot. Photos by Yun-He Wu.

on floor of mouth; supratympanic ridge distinct with reddish-brown pigmentation, extending from posterior corner of eye to supra-axillary gland, the posterior end of supratympanic ridge not expanded (Fig. 3).

Forelimb relatively long, forearm shorter than hand, not enlarged (FAL 7.3 mm, HL 7.6 mm); fingers slender, relative finger lengths: I = IV < II < III; tips of fingers rounded, slightly swollen; subarticular tubercles absent on fingers; supernumerary tubercles absent; webbing between fingers absent; inner metacarpal tubercle large and rounded, separated from the smaller, round outer metacarpal (Fig. 3E).

Hindlimbs relatively long; thigh length greater than tibia length (TL/THL 92.4%) and foot length (FL/THL 95.8%); tibiotarsal articulation reaches the nostril when hindlimb is stretched along the side of the body; heels overlapping when thighs are positioned at right angles to the body; relative toe lengths: I < II < V < III < IV; tips of toes rounded, slightly swollen; subarticular tubercles distinct under the base of I, II, III, and IV toes; rudimentary webbing between toes; narrow lateral fringes present on all toes; inner metatarsal tubercle elongated (IMTL 1.4 mm, 5.0% SVL), outer metatarsal tubercle absent (Fig. 3F).

Dorsal skin relatively smooth; tiny white tubercles scattered on flanks; oval supra-axillary gland raised, located in axillary region dorsally from insertion of forelimb, approximately 0.8 mm in diameter; ventral skin smooth; pectoral gland laterally compressed, 1.0 mm in diameter; oval femoral glands distinct on posteroventral surface of thigh, approximately 0.9 mm in diameter, located on posteroventral surfaces of thighs, closer to knee than to vent; ventrolateral glands, distinctly visible, raised, forming an incomplete line (Fig. 3).

Color of the holotype in life. Dorsal surface of body brown, with distinct, black, inverted triangular pattern between the anterior corners of the eyes in connection with a dark brown W-shaped marking in the interorbital region, which is also connected to a W-shaped marking between the axillae; wide dark brown bars in upper lip, with distinct white spots; canthus rostralis reddish; flanks with large irregular black flecks and several small light tangerine tubercles; supratympanic ridge reddish and a large black marking under supratympanic ridge; tympanum bicolored, with the upper 2/3 of the tympanum dark brown and the lower 1/3 light brown; elbow to upper arm and tibio-tarsal articulation distinctly coppery orange in color on the dorsum; transverse black bars on dorsal surfaces of fingers and toes, lower arms, tarsus, thighs and tibia; iris distinctly bicolored, typically orange in upper half, silver white in lower half, with black reticulations throughout; ventral surface of throat, chest, and belly creamy white; chest and abdomen with distinct dark patches; ventral surface of head and limbs greyish purple; ventral surface of limbs scattered with creamy white spots and small patches; pectoral and femoral glands creamy white, supra-axillary glands light orange (Fig. 3 and Suppl. material 4).

Table 1. Measurements (in mm) of the type series of *Leptobrachella weixinensis* sp. nov. Bold font and an asterisk (*) indicate the holotype.

	NNU 040615*	**NNU 040603**	**NNU 040602**
Sex	Male	Male	Male
SVL	28.2	28.5	29.7
HDL	10.0	10.6	10.6
HDW	10.1	10.1	10.6
SNT	3.8	3.9	3.9
INS	2.4	2.3	2.4
IOD	3.3	3.5	3.7
UEW	2.8	2.8	2.7
ED	3.6	3.6	3.9
TD	1.8	2.3	2.1
TED	1.0	1.0	1.1
SN	1.5	1.5	1.4
DNE	1.6	1.7	1.8
IFE	4.5	4.8	4.8
IBE	8.3	8.6	8.9
FAL	7.3	6.8	7.4
HL	7.6	7.0	7.7
THL	14.4	14.3	15.2
TL	13.3	12.7	13.8
TOL	7.8	7.1	7.8
FL	13.8	12.8	14.2
IMTL	1.4	1.6	1.6
FL1	2.8	2.8	2.8
FL2	3.4	3.0	3.2
FL3	5.5	4.9	5.3
FL4	2.8	2.7	2.7
TL1	2.2	2.1	2.5
TL2	2.9	2.8	2.9
TL3	4.6	4.6	5.2
TL4	8.0	7.8	8.3
TL5	4.1	4.0	4.1

Color of holotype in preservative. After three months of storage in 70% alcohol, the dorsum and limb surfaces fading to uniform light brown, except for upper arm; upper arm surface copper brown; transverse bars on limbs still distinct; ventral surface of limbs, chest, abdomen, and throat greyish white; pectoral, femoral, supra-axillary, and ventrolateral glands greyish white; subarticular tubercles, metacarpal tubercles, and metatarsal tubercle fading to gray (Fig. 4).

Distribution and ecology. At present, this species is known to be distributed only in its type locality, that is, the mountains around Shizigou Village, Zhaxi Town, Weixin County, with an altitude of 1280–1400 meters. During the breeding season, it gathers in mountain streams with a width of 1.5–2 meters, surrounded by typical subtropical evergreen broad-leaved forests and bamboo forests (Fig. 5). The stream has a steep slope and low water temperature. There are often waterfalls and pools. The banks are covered with lush plants, mainly grasses. The village can be seen about 1 km away from the stream. Species that inhabit the same environment include *Nanorana yunnanensis* and *Bufo andrewsi*.

During a field survey in mid-June, male toads were heard chirping in the cracks of huge rocks or under grass leaves beside streams. The chirping sound was like a cricket and varied. When not disturbed, the chirping sound consisted of two syllables, with an interval of about 0.5 seconds between each segment. When stimulated by light or someone passing by, the chirping sound changed to a long single syllable. After the environment stabilized, the chirping sound gradually returned to its former state. If further stimulated, such as by direct light, the toad stopped chirping, shrank into the cracks of the rocks, or crouched until it felt that the surrounding environment was safe. However, no tadpoles were observed during this period, nor were female toads.

Comparisons. Phylogenetically, the matrilineal genealogy assigns *Leptobrachella weixinensis* sp. nov. to *L. oshanensis* complex (clade A). Thus, we compared *Leptobrachella weixinensis* sp. nov. to all other recognized species of *L. oshanensis* complex from clade A, which include *L. bijie*, *L. jinyunensis*, *L. chishuiensis*, *L. suiyangensis*, *L. jinshaensis*, *L. purpuraventra*, *L. bourreti*, *L. dong*, *L. dushanensis*, *L. graminicola*, *L. yeae*, *L. wulingensis*, *L. dorsospina*, *L. yunyangensis*, *L. niveimontis*, *L. alpina*, *L. purpurus*, *L. eos*, *L. oshanensis*, *L. murphyi*, *L. korifi*, *L. sinorensis*, and *L. tengchongensis* (e.g., Ohler et al. 2011; Yang et al. 2016, 2018; Wang et al. 2019, 2020; Chen et al. 2020, 2021; Li et al. 2020, 2024; Luo et al. 2020; Cheng et al. 2021; Nguyen et al. 2021; Shi et al. 2021; Luo et al. 2022; Chen et al. 2023; Liu et al. 2023; Matsui et al. 2023; Shi et al. 2023; Suppl. material 3).

Leptobrachella weixinensis sp. nov. is significantly different from *L. jinyunensis* by tibiotarsal articulation reaches the nostril (vs. reaches the level of the middle of the eye), subarticular tubercles distinct under the base of I, II, III and IV toe (vs. absent), dorsal skin relatively smooth (vs. dorsal skin rough with large tubercles in size of humeral glands, without conical spines), iris distinctly bicolored, typically orange in upper half, silver white in lower half (vs. iris gold above, gradually silver bellow), and heels overlapping when thighs are positioned at right angles to the body (vs. heels slightly contact with each other); from *L. bijie* by interorbital distance wider than internarial distance (vs. internarial distance equal to interorbital distance), tibiotarsal articulation reaches the nostril (vs. reaches the region between middle of eye to anterior corner of eye), heels overlapping when thighs are positioned at right angles to the body (vs. heels just meeting), and flanks with large irregular black flecks (vs. flanks with several dark blotches, longitudinally in two rows); from *L. chishuiensis* by interorbital distance wider than internarial distance (vs. interorbital distance shorter than internasal distance), tibiotarsal articulation reaches the nostril (vs. reaches the tympanum), upper margin of tympanum incontact with supratympanic ridge (vs. upper margin of tympanum in contact with supratympanic ridge), and relative finger lengths: I ≈ IV < II < III (vs. relative finger lengths: II < IV < I < III); from *L. suiyangensis* by tibiotarsal articulation reaches the nostril (vs. reaches to the anterior eye), heels overlapping when thighs are

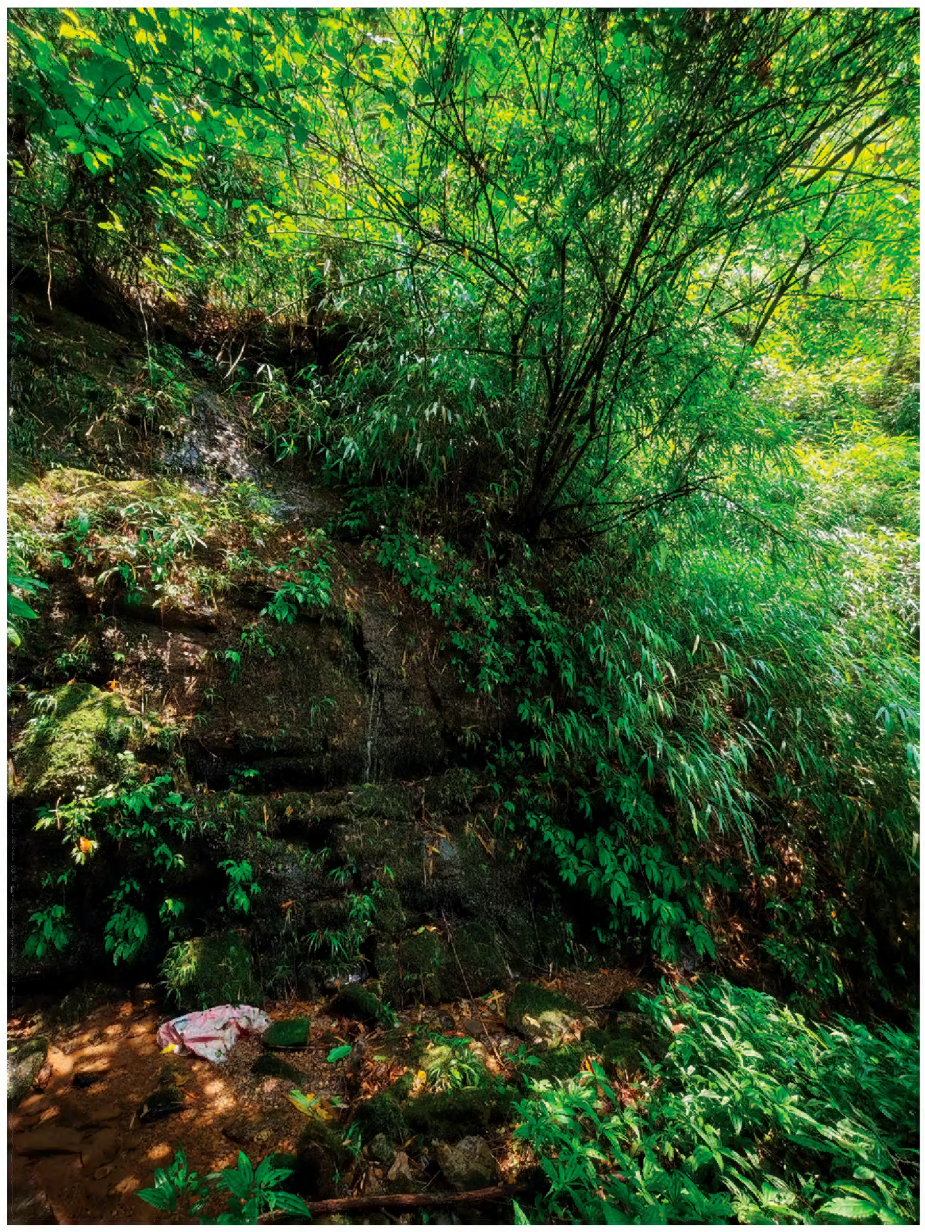

Figure 5. Habitat at the type locality of *Leptobrachella weixinensis* sp. nov. at Shizigou village, Weixin County, Yunnan Province, China. (Photo by Lu Chen)

positioned at right angles to the body (vs. heels meeting each other), subarticular tubercles distinct under the base of I, II, III and IV toe (vs. absent), dorsal skin relatively smooth (vs. dorsal skin is shagreened and scattered with fine and rounded granules), and relative finger lengths: I ≈ IV < II < III (vs. relative finger lengths: I < II < IV < III); from *L. jinshaensis* by tibiotarsal articulation reaches the nostril (vs. tibiotarsal articulation reaches middle eye), rudimentary webbing between toes (vs. toes without webbing), upper margin of tympanum incontact with supratympanic ridge (vs. upper margin of tympanum in contact with supratympanic ridge), dorsal skin relatively smooth (vs. dorsal skin shagreened, some of the granules forming longitudinal short skin ridges), and subarticular tubercles distinct under the base of I, II, III and IV toe (vs. absent); from *L. purpuraventra* by tibiotarsal articulation reaches the nostril (vs. reaches the middle of eye), dorsal skin relatively smooth (vs. dorsal skin shagreened, some of the granules forming longitudinal short skin ridges), ventral surface of throat, chest, and belly creamy white, chest and abdomen with distinct dark patches (vs. ventral surface grey purple, with distinct or indistinct nebulous greyish speckling on chest and ventrolateral flanks), and subarticular tubercles distinct under the base of I, II, III and IV toe (vs. absent); from *L. dong* by narrow lateral fringes present on all toes (vs. toes with wide lateral fringes), tibiotarsal articulation reaches the nostril (vs. reaches the middle of eye), upper margin of tympanum incontact with supratympanic ridge (vs. upper margin of tympanum in contact with supratympanic ridge), and relative finger lengths: I ≈ IV < II < III (vs. relative finger lengths: II < I < IV < III); from *L. dushanensis* by narrow lateral fringes present on all toes (vs. wide lateral fringes present on all toes), upper margin of tympanum incontact with supratympanic ridge (vs. upper margin of tympanum in contact with supratympanic ridge), relative finger lengths: I ≈ IV < II < III; (vs. relative finger lengths: II < I < IV < III), and tibiotarsal articulation reaches the nostril (vs. reaches interior corner of the eye); from *L. graminicola* by SVL 28.2–29.7 mm in three males (vs. 23.1–24.6 mm in six adult males), narrow lateral fringes present on all toes (vs. toes with broad lateral fringes), subarticular tubercles distinct under the base of I, II, III and IV toe (vs. absent), and ventral surface of throat creamy white without spot (vs. throat dark brown with light grey-brown flecks and spots); from *L. yeae* by relative finger lengths: I ≈ IV < II < III (vs. relative finger lengths: II < I < IV < III), tibiotarsal articulation reaches the nostril (vs. reaches the middle eye), pectoral gland distinct (vs. indistinct), and subarticular tubercles distinct under the base of I, II, III and IV toe (vs. absent); from *L. wumingensis* by tongue with shallow notch at posterior tip (vs. tongue with a deep notch at posterior tip), toes with rudimentary webbing and narrow lateral fringes (vs. absence of toe webbing and lateral fringes), subarticular tubercles distinct under the base of I, II, III and IV toe (vs. absent), tibiotarsal articulation reaches the nostril (vs. reaches the middle eye), and heels overlapping (vs. heels meeting); from *L. dorsospina* by relative finger lengths: I ≈ IV < II < III (vs. relative finger lengths: II = IV < I < III), dorsal skin relatively smooth (vs. dorsal skin rough, with dense conical granules, tubercles, glandular folds and conical spines), tibiotarsal articulation reaches the nostril (vs. reaches the posterior corners of eyes), and black spots on irregular on flanks (vs. black spots on flanks in two rows); from *L. yunyangensis* by tibiotarsal articulation reaches the nostril (vs. reaches to the anterior corner of the eye), relative finger lengths: I ≈ IV < II < III (vs. relative finger lengths: I < II = IV < III), upper margin of tympanum incontact with supratympanic ridge (vs. upper margin of tympanum in contact with supratympanic ridge), tongue with shallow notch at posterior tip (vs. tongue cordiform, deeply notched behind), and dorsal skin relatively smooth (vs. dorsal skin rough, with sparse large granules and tubercles and short longitudinal ridges on the shoulder); from *L. niveimontis* by SVL 28.2–29.7 mm in three males (vs. 22.5–23.6 mm in four adult males), heels overlapping (vs. heels meeting), and throat, chest, and belly creamy white, chest and abdomen with distinct dark patches (vs. black and bluish-white marbling all over ventral surfaces of throat, chest and belly, denser on throat than on chest and belly); from *L. purpurus* by narrow lateral fringes present on all toes (vs. toes with wide lateral fringes), dorsal surface of body brown (vs. dorsum coloration purplish brown in life), iris bicolored, typically orange in upper half, silver white in lower half (vs. iris bicolored, upper half orange yellow, lower half sliver white), and tibiotarsal articulation reaches the nostril (vs. reaches to posterior corner of the eye); from

L. alpina by narrow lateral fringes present on all toes in males (vs. toes with wide lateral fringes in males), tibiotarsal articulation reaches the nostril (vs. reaches to anterior corner of the eye), and head longer than wide (vs. approximately equal); from *L. oshanensis* by narrow lateral fringes present on all toes (vs. toes without lateral fringes), subarticular tubercles distinct under the base of I, II, III and IV toe (vs. absent), tongue with shallow notch at posterior tip (vs. tongue with a deep notch at posterior tip), interorbital distance wider than internarial distance (vs. interorbital distance distance equal to internarial), and pectoral glands distinct (vs. invisible); from *L. eos* by a smaller body size, SVL 28.2–29.7 mm in three males (vs. 33.1–34.7 mm in six adult males), supratympanic fold prominent (vs. absent), narrow lateral fringes present on all toes (vs. toes with wide lateral fringes), flanks with large irregular black spots (vs. absent), and iris bicolored, typically orange in upper half, silver white in lower half (vs. iris orange above, light golden below); from *L. bourreti* by nostril closer to tip of snout than to anterior margin of eye (vs. nostrils closer to eye than to tip of snout), femoral and ventrolateral glands distinct (vs. femoral glands and ventrolateral gland indistinct), vocal sac openings slit-like, paired, located posterolaterally on floor of mouth (vs. no opening on mouth floor), and interorbital distance wider than internarial distance (vs. internarial distance equal to interorbital distance); from *L. murphyi* by SVL 28.2–29.7 mm in three males (vs. 23.2–24.9 mm in ten adult males), narrow lateral fringes present on all toes (vs. wide lateral fringes present on all toes), heels overlapping (vs. heels meeting), and dorsal skin relatively smooth (vs. dorsal skin relatively rough with small tubercles and short folds with reddish tips); from *L. korifi* by tibiotarsal articulation reaches the nostril (vs. reaches anterior corner of eye), and interorbital distance slightly wider than internarial distance (vs. internarial distance equal to interorbital distance); from *L. sinorensis* by tibiotarsal articulation reaches the nostril (vs. reaches center of eye), and dorsal surface of body brown, without pink dots (vs. light brown dorsally on head and body, with dark spots, partly dotted with pink); from *L. tengchongensis* by SVL 28.2–29.7 mm in three males (vs. 23.9–26.0 mm in five adult males), ventrolateral glands distinct (vs. ventrolateral glands indistinct), dorsal skin relatively smooth (vs. skin on dorsum shagreened and scattered with fine, round tubercles), and iris distinctly bicolored, typically orange in upper half, silver white in lower half, with black reticulations throughout (vs. iris not bicolored, uniformly dark brown and scattered with minute, coppery reticulations throughout).

Discussion

The diversity of amphibians is greatly underestimated in the Northeastern Hills of Yunnan, China. In recent years, many new amphibian species, especially from the genus *Leptobrachella*, have been described in Sichuan and Guizhou provinces, such as *L. bijie*, *L. dong*, *L. jinshaensis*, *L. yeae*, and *L. jinyunensis* (e.g., Wang et al. 2019; Cheng et al. 2021; Shi et al. 2021, 2023; Liu et al. 2023; AmphibiaChina 2025; Frost 2025). Compared to the other two neighboring provinces in the Wumeng Mountain region, the diversity of *Leptobrachella* in the Northeastern Hills of Yunnan has attracted less attention, and no new species have been described in the region in recent years. A large number of newly recorded species have been found along provincial boundaries in recent years (e.g., Cao et al. 2024; Liu et al. 2023; He et al. 2023). The Northeastern Hills of Yunnan lie at the border of two provinces where many new species have recently been described, indicating that the region's diversity has not been fully documented. Future efforts should focus on strengthening fieldwork and research to better document and understand species diversity in this region.

Combining morphological and molecular lines of evidence, our present work describes the Zhaotong population as a new species. Our results bring the total number of *Leptobrachella* species to 111, and the number of *Leptobrachella* species known from China to 47 (AmphibiaChina 2025; Frost 2025). Among these, 17 species of *Leptobrachella* are now known to occur in Yunnan Province, China, which include: *L. alpina*, *L. pelodytoides*, *L. ventripunctata*, *L. tengchongensis*, *L. albomarginata*, *L. yingjiangensis*, *L. purpurus*, *L. eos*, *L. bourreti*, *L. nyx*, *L. niveimontis*, *L. flaviglandulosa*, *L. feii*, *L. dorsospina*, *L. aspera*, *L. pingbianensis*, and *L. weixinensis* sp. nov. (Yuan et al. 2022; AmphibiaChina 2025; Wu et al. 2025).

Our results also reveal that *L. bijie* collected in Chishui, Guizhou Province and *L. chishuiensis* from the type specimens cluster together, which is consistent with the results of Wang et al. (2022). Wang et al. (2022) discussed in detail the classification of these two species based on morphological and molecular systematics, and speculated that *L. chishuiensis* should most likely be considered conspecific with *L. bijie* (and be synonymized). In addition, Shi et al. (2023) reported that *L. jinyunensis* first forms a sister clade with *L. bijie*, and this clade subsequently forms a sister group with *L. chishuiensis*. However, our results indicate that *L. bijie* is paraphyletic; thus, the validity of *L. jinyunensis* requires further investigation. Both *L. chishuiensis* and *L. jinyunensis* were described as new species based on haplotype network analyses of nuclear data. However, this method alone may be prone to error and might not provide sufficient resolution for reliable species delimitation. We therefore recommend that future studies employ genome-level data and population genomics approaches, combined with extensive sampling, to resolve this question.

Acknowledgments

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Supplementary material 1

Localities and voucher data for all specimens used in this stud

Authors: Nai-Yi Liu, Lu Chen, Wei Xu, Yun-He Wu
Data type: xlsx
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Link: https://doi.org/10.3897/zse.101.148507.suppl1

Supplementary material 2

Average uncorrected *p*-distances among *Leptobrachella* species

Authors: Nai-Yi Liu, Lu Chen, Wei Xu, Yun-He Wu
Data type: xls
Explanation note: Average uncorrected p-distances (percentage) among *Leptobrachella* species calculated from 16S rRNA gene sequences (below the diagonal) and standard error estimates (above the diagonal). The ingroup mean uncorrected p-distances are shown on the diagonal.
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Link: https://doi.org/10.3897/zse.101.148507.suppl2

Supplementary material 3

Selected diagnostic characters for species described herein and species in the genus *Leptobrachella*

Authors: Nai-Yi Liu, Lu Chen, Wei Xu, Yun-He Wu
Data type: xls
Explanation note: Selected diagnostic characters for species described herein and species in the genus *Leptobrachella* occurring north of the Isthmus of Kra (modified from Rowley et al. 2017; Yuan et al. 2017; Yang et al. 2018; Wang et al. 2018; Chen et al. 2024; Wu et al. 2024).
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Link: https://doi.org/10.3897/zse.101.148507.suppl3

Supplementary material 4

Ventral surface of the fingers for *Leptobrachella weixinensis* sp. nov.

Authors: Nai-Yi Liu, Lu Chen, Wei Xu, Yun-He Wu
Data type: jpg
Explanation note: **A.** NNU 040615, **B.** NNU 040603, and **C.** NNU 040602.
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Link: https://doi.org/10.3897/zse.101.148507.suppl4